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Research Article

Competitive superiority of non-native invaders becomes weaker when plant diversity increases – a case study with *Solidago* species

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Abstract

Two popular hypotheses in invasion biology are the "inherent superiority hypothesis", stating that non-native species generally perform better than native species, and the "biotic resistance hypothesis", stating that at local scale invasibility decreases with resident species richness. To test if plant community diversity reduces the performance of invasive non-native species more strongly than that of native ones, individuals of three *Solidago* species, *S. virgaurea* (native), *S. canadensis* (non-native, frequent in the local flora) and *S. gigantea* (non-native, non-frequent in the local flora), were planted into 80 experimental grassland communities varying in plant species richness (1, 2, 4, 8, 16, and 60 species) and functional group number (1 to 4 functional groups) (Jena Experiment, Germany). Survival was monitored and growth-related traits were studied as performance measures over two growing seasons. Both non-native invasive *Solidago* species grew faster than the native one. At low species richness, the non-native invasive *S. canadensis* and *S. gigantea* produced more biomass and had taller shoots with more leaves than the native *S. virgaurea*. This was presumably due to their better capability to take advantage of unused resources, supporting the inherent superiority hypothesis. With increasing sown plant species richness associated with a denser and taller canopy of the grasslands, survival and individual plant performance decreased in all three *Solidago* species, which is in line with the biotic resistance hypothesis. The decline in growth performance with increasing species richness was particularly pronounced in the non-native *S. canadensis* and *S. gigantea* so that their inherent superiority was more weakened compared to the native *S. virgaurea* with increasing plant diversity. These results emphasize the important role of native plant diversity for invasion resistance at local scale.

Key words: Biodiversity, functional traits, invasiveness, invasion resistance, plant performance, specific leaf area

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Introduction

Biodiversity and ecosystem functions are threatened by various global change drivers, and biological invasions are one of the major components of global environmental change (Pejchar and Mooney 2009; Vilà et al. 2011; van Kleunen et al. 2015). The process of biological invasion is a complex phenomenon driven by various interactive processes. The probability for successful invasion of a species is on the one hand influenced by inherent biological characteristics of the invader

that determine its invasiveness, and on the other hand by the environmental characteristics of the invaded ecosystem and biotic interactions with the recipient community that determine its invasibility (Alpert et al. 2000; Gioria et al. 2023).

Regarding species invasiveness, the inherent superiority hypothesis (Lowry et al. 2013; Sheppard and Lüpke 2024) suggests in the broadest sense that certain traits of the non-native species make them more likely to successfully establish and reach a generally higher performance in the new environment compared to native species. There are multiple possible mechanisms related to inherent superiority, which also depend on the stage of invasion (Dawson et al. 2009), and different performance measures like individual plant size and growth, survival, and reproduction, as well as responses to environmental variation, natural enemies or mutualists, have been used to assess the higher performance of non-native species compared to native species (Sheppard and Lüpke 2024). Particularly, traits promoting high reproduction rates and rapid spread are important for the successful introduction into a new environment (e.g. Lowry et al. 2013). Once an invader has entered a community, traits that enable efficient use of resources and rapid growth are decisive for invasion success. Thus, successful invaders are often species with high relative growth rates, a high specific leaf area (related to faster growth rates) and taller growth in high resource environments (Leishman et al. 2007; van Kleunen et al. 2010).

A further common idea to explain the invasion success of non-native species is their high trait plasticity allowing them to achieve a high performance under different environmental conditions (Richards et al. 2006; Davidson et al. 2011). While some studies have demonstrated higher trait plasticity of non-native invasive species (e.g. Davidson et al. 2011), others found that phenotypic plasticity was similar in non-native invasive and native species (Palacio-López and Gianoli 2011; Godoy et al. 2011), suggesting that they are equally capable of showing plastic responses to environmental variation. Under high resource availability, competition for light is considered as one important determinant for the successful establishment of an invader (Gioria and Osborne 2014). Superiority in light competition can be achieved by having a taller growth or higher specific leaf area than competing native species, but there is little evidence that non-native invasive species show a greater plasticity in these traits (Palacio-López and Gianoli 2011; van Kleunen et al. 2011). However, most comparisons have been made to test plasticity in response to resource availability, while comparisons of trait plasticity of non-native invasive and native species within the same plant community are scarce (Hulme and Bernard-Verdier 2017).

The biotic resistance hypothesis (Elton 1958) predicts that more species-rich communities are more resistant to invasion at local scale. Communities with higher species richness are thought to use a greater share of the available nice space by using resources more completely and creating a more competitive environment (Naeem et al. 2000; Tilman 2004). Moreover, higher species richness increases the probability to include species that are particularly invasion-suppressive (Wardle 2001). Although invasion biology mainly focuses on non-native species, the process of invasion can be broadly defined to also refer to native species as those can also invade communities (Valéry et al. 2008). A number of experimental studies addressing diversity-invasion resistance relationships have used native plant species as surrogates for invaders and showed that increasing plant diversity limits the establishment, performance and survival of newly colonizing (invading) plant species (e.g. Mwangi et al. 2007; Nitschke et al. 2010). However, recipient communities of native plants might be less resistant to non-native invasive plants due

to the lack of co-evolutionary history (Saul et al. 2013), but this has rarely been tested so far (but see Sun et al. 2015).

The present study was conducted in a biodiversity experiment (Jena Experiment) with 80 grassland communities varying in sown plant species richness (1, 2, 4, 8, 16, and 60 species) and functional group number (1 to 4 functional groups) (Roscher et al. 2004). Because trait differences among species may strongly depend on taxonomic relatedness (Pyšek 1998) and growth form (van Kleunen et al. 2010), the comparison of non-native with native species of the same genus or family and with similar growth forms has been suggested as a convenient approach in invasion studies with a limited number of species (Vilà and Weiner 2004; van Kleunen et al. 2010). Therefore, three species of the genus *Solidago* (Asteraceae) with similar growth forms were chosen for the experiment, planted in all communities and studied over two growing seasons. They represented two non-native invasive species, namely *S. canadensis* L. (= locally common invasive; frequent in the local flora) and *S. gigantea* Aiton (= locally rare invasive; non-frequent in the local flora), and one native species (*S. virgaurea* L.). Existing studies comparing the native *S. virgaurea* with both non-native invasive goldenrod species showed that the non-native species produced more biomass and were better competitors than the native species as single individuals or in pairwise interactions, but did not show a greater plasticity to different soil conditions than the native *S. virgaurea* (Szymura and Szymura 2015, 2016; Szymura et al. 2019). However, so far it is not clear whether the non-native invasive *S. canadensis* and *S. gigantea* and the native *S. virgaurea* vary in their invasiveness into communities of increasing plant diversity. Previous studies have shown that more diverse plant communities of the Jena Experiment produce more biomass, have a taller and denser canopy, and use soil resources more completely (reviewed in Weisser et al. 2017). Therefore, the following hypotheses were tested: (1) Survival and individual plant performance differ among the study species. Under the assumption that particular characteristics of non-native species cause them to perform better than native species, I expected that survival and growth performance would be highest in the non-native, locally common invasive *S. canadensis*, slightly lower in the non-native, locally rare invasive *S. gigantea* and lowest in the native *S. virgaurea*. (2) Survival and performance of the three study species decrease with increasing sown species richness of the experimental grassland communities. I expected that the decline would be stronger for the non-native invasive species *S. canadensis* and *S. gigantea* because they are better able to capitalize on unused resources at low sown plant diversity, where they reach a greater performance, while they have no advantage at high sown plant diversity and do not show greater plasticity in traits related to light acquisition.

Methods

Jena Experiment

The Jena Experiment (Suppl. material 1: fig. S1) is located in the alluvial plain of the Saale river in Jena (Germany, 50°55'N, 11°35'E, 130 m a.s.l.) (Roscher et al. 2004). Mean annual temperature is 10.4 °C, and average annual precipitation amounts to 593 mm (1990–2020; Jena-Sternwarte, https://www.dwd.de). The soil is a Eutric Fluvisol developed from up to 2-m-thick fluvial sediments that are almost free of stones. Due to the fluvial dynamics of the river Saale, soil texture

varies from sandy loam near the river to silty clay with increasing distance from the river. The area was converted from grassland to arable land in the early 1960s and had been managed as highly fertilized agricultural field for the last 40 years prior to the establishment of the biodiversity experiment. The field had been kept fallow in the year before sowing, harrowed bimonthly, and treated with glyphosate (Round-up, Monsanto, St. Louis, Missouri, USA) in July 2001. The experimental plant communities were sown with a total density of 1000 viable seeds per m^2 in early May 2002. Sixty plant species typical for mesophilic grasslands of the region served as species pool for the biodiversity experiment. These species were classified into four functional groups: 16 grasses, 12 legumes, 20 tall herbs and 12 small herbs (for a species list see Suppl. material 1: table S1). Plant diversity of the experimental communities was varied as species richness (1, 2, 4, 8, 16, and 60 species) and functional group number (1, 2, 3, and 4 functional groups) in a near-orthogonal design (Suppl. material 1: table S2). The species compositions for each plant community were randomly assembled from the respective functional groups. In mixtures, all species were sown with equal proportions. In total, 82 plant communities were established on plots of 20 × 20 m size (reduced to 6 × 6 m in 2010). Plots were arranged in four blocks parallel to the riverside to account for the gradient in soil texture. Sown species-richness levels were represented by 16 replicates each, except for the 16-species mixtures with 14 replicates (no mono-functional small herb and legume mixture was possible at this species-richness level), and the 60-species mixture with four replicates. Moreover, two monoculture plots were abandoned after several years due to poor establishment, and therefore only 14 monoculture plots were available. The plant communities were maintained by manual weeding three times per year. The plots were mown and mown biomass was removed twice per year (June, September) according to the traditional management of extensive grasslands in the study region. Plots did not receive any fertilizer. More details on the design and maintenance of the biodiversity experiment can be found in Roscher et al. (2004) and Weisser et al. (2017).

Study species

Goldenrod species from North America are globally successful invader species. In Central Europe, *S. canadensis* L. (Canadian goldenrod) and *S. gigantea* Aiton (Giant goldenrod) belong to the most widespread non-native *Solidago* species. Both species have been introduced more than 250 years ago in Europe and became invasive some 100 years later (Weber 1998). In Europe both species grow in similar habitats, such as fallow land, ruderal sites, roadsides, or grasslands (Weber and Jakobs 2005). *Solidago virgaurea* L. is native to Europe, northern Africa and western Asia (Wagenitz 1979). In the study region, *S. canadensis* (= locally common invasive) is frequent in the local flora around Jena. The species occasionally occurs as a weed in the plots of the Jena Experiment and was a dominant species in the early years in two unmanaged succession plots (Roscher et al. 2016). *Solidago gigantea* (= locally rare invasive) is less frequent in the flora around Jena (Korsch et al. 2002) and has not been found on the experimental site so far. The native *S. virgaurea* L. (= native) grows naturally in calcareous grasslands and warmth-loving hems in the Central Saale valley around Jena (Korsch et al. 2002). All species are rhizomatous perennials; their shoots are annual and newly sprout in spring, and grow as single stems up to the inflorescence, but non-flowering leaf rosettes are also often present.

Phytometer experiment

Seed material of the non-native *Solidago* species was collected from natural populations from at least ten different individuals. Seeds of the locally common invasive *S. canadensis* were collected from a population in Central Germany (near Bad Blankenburg; Thuringia) and a population in Southern Germany (near Constance; Baden-Württemberg). Seeds of the locally rare invasive *S. gigantea* were collected from a population in Southern Germany (near Constance; Baden-Wuerttemberg). Seeds of the native *S. virgaurea* (from Central Germany) were purchased from a commercial supplier (Rieger-Hofmann GmbH) that propagates seeds from natural populations. Because seeds of *S. gigantea* were not available from Central Germany, two provenances of *S. canadensis* were used to account for possible regional effects.

Starting in early January 2011, seeds were pre-germinated on moistened filter paper. Between 21 January and 10 February 2011, seedlings were individually transferred to QuickPot™ 35 trays of 183 cm^3 volume (Hermann Meyer KG, Rellingen, Germany) filled with topsoil collected from the field site mixed with 30 vol% mineral sand. The trays were cultivated in a greenhouse (16 h day at 15 °C, 8 h night at 10 °C) for approximately eight weeks. In early April, trays were transferred to an open greenhouse with ambient light and temperature conditions to harden the plants for approximately three weeks before they were transported to the field site shortly before planting. Two individuals of each species (and provenance in case of *S. canadensis*), i.e. eight individuals in total, were planted into a subplot of one square meter size in each of the 80 plots of the biodiversity experiment (as described above) between 25 to 29 April 2011. The individuals were planted in a regular grid (three rows with two or three plants each with 0.25 m distance), and the eight grid positions were randomly assigned to each species in each plot (Suppl. material 1: fig. S1). In total, 640 individuals were planted and marked with a white plastic label. Individuals were watered twice a week for three weeks until the first major rainfall event occurred to help with establishment. After mowing in early June, all individuals were assessed for survival. Those that did not survive the establishment phase (in total 19 out of 640 plants) were replanted between 21 June and 16 July 2011. Afterwards, dead plants were no longer replaced.

Stretched shoot length was measured and the number of leaves was counted for each individual when planting to assess initial size. In August 2011 and 2012, individuals were assessed for survival and growth (by counting the number of shoots and total number of leaves). Relative leaf production rate (RLPR) was calculated as

$$RLPR = \frac{log(L_2) - log(L_1)}{t_2 - t_1} \quad \text{(eqn. 1)},$$

where L is the number of leaves and t is the time span in months between two monitoring dates (Schlaepfer et al. 2010). RLPR was calculated for three intervals: as a measure of growth since planting (April 2011 to August 2012) and to compare the first and the second growing season (April to August 2011, and August 2011 to August 2012). Furthermore, the stretched length of the longest shoot and the canopy height of the surrounding vegetation in the immediate vicinity of each phytometer individual were measured with a ruler. Leaf greenness (unitless), an estimate of chlorophyll concentration, was assessed by measuring the transmittance of two different wavelengths (650 nm and 940 nm) with a portable chlorophyll

meter (SPAD-502, Konica-Minolta, Osaka, Japan) on three young but fully expanded leaves per individual and averaged. Measured leaf greenness values of the chlorophyll meter and chlorophyll concentrations (per leaf area) from leaf extracts (extraction according to Moran 1982) sampled from all *Solidago* species were strongly correlated (r^2 = 0.869, P < 0.001, N = 80). Moreover, a sample of 3 to 10 fully developed leaves (dependent on leaf number and availability) was collected, scanned with a flatbed scanner (Epson Perfection, V600 Photo), dried at 70 °C for 48 h and weighed. Scanned leaves were analyzed with image software (Gimp2; https://docs.gimp.org) to derive leaf area and maximum leaf length. Specific leaf area (SLA) was computed by dividing leaf area (mm^2) by leaf dry mass (mg). Finally, in August 2012, the occurrence of inflorescences was recorded, and all surviving plants were harvested at ground level. Basal stem diameter of the longest shoot was measured with callipers. Individual plant biomass was determined after drying (70 °C, 48 h). During both measurement campaigns in August 2011 and 2012, community leaf area index was measured with a LAI-2000 plant canopy analyzer (LI-COR, Nebraska, USA). All data is publicly available (Roscher 2025a, 2025b).

Data analyses

Statistical analysis was conducted with the statistical software R (version 4.2.3, R Core Team 2019; http://www.Rproject.org). Linear mixed-effects models applying the *lmer* function in the R library *lme4* (Bates et al. 2015) were used for analyses of all continuous measured variables, while survival, reproductive stage and shoot number were analysed with a generalized linear model (GLM). Starting from an intercept-only model with plot nested in block as random effects, sown species richness (as log-linear term), functional group number (as linear term), identity of *Solidago* species (as a factor), the interaction between sown species richness and species identity, and the interaction between functional group number and species identity were sequentially added as fixed effects. The model was extended for variables measured in both study years by adding year and the interaction of year with the previously named terms as further fixed effects and the identity of the individual plant as a further random effect nested in plot. Models were fitted with the maximum likelihood method (ML) and likelihood ratio tests (χ^2 ratio) were used to test for a statistically significant improvement of the models after step-wise addition of the fixed effects. The R library *emmeans* (Lenth 2024) was used to test for significant differences among species in the mean values of the measured variables and the strengths of their responses to sown species richness (i.e. standardised regression slopes). In a first set of models, both provenances of *S. canadensis* were treated separately (i.e. the factor species identity had four levels). Because these models showed hardly any differences in the measured variables between both provenances of *S. canadensis* (with the exception of RLPR and leaf greenness in the first growing season), they were pooled in the final set of models (i.e. the factor species identity had three levels) because differences among species were the main focus of the analyses.

Results

Nearly all individuals (99%) survived the year of planting. In the second year, survival of the locally rare invasive *S. gigantea* (94%) was greater than that of the locally common invasive *S. canadensis* (83%) and the native *S. virgaurea* (80%).

Survival in the second year varied with sown species richness and functional group number of the plant communities (Table 1). Sown plant species richness had negative effects on the survival of *S. canadensis*, and no consistent effect on the survival of *S. gigantea* and *S. virgaurea* (Table 1, Suppl. material 1: fig. S2). Increased functional group number generally decreased survival. One year after planting, 18% of *S. virgaurea* individuals were flowering, but only 6% of *S. gigantea* and 8% of *S. canadensis* individuals formed inflorescences. Increasing sown plant species richness had negative effects on the formation of inflorescences (Table 1).

Relative leaf production rates (RLPR) estimated from the number of leaves over the whole study period from planting until the final harvest was greater in both non-native *Solidago* species than in the native *S. virgaurea* (Table 2). RLPR generally decreased with sown species richness (Table 1). Negative effects of increasing species richness on RLPR were stronger in the locally common invasive *S. canadensis* than in the locally rare invasive *S. gigantea*, but did not differ significantly from the native *S. virgaurea*. In the year of planting, RLPR were greatest in *S. canadensis* and decreased in the order *S. canadensis* > *S. gigantea* > *S. virgaurea*. The negative effects of increasing sown species richness on RLPR were similar in all *Solidago* species (Fig. 1a, Table 2). From the first to the second year, RLPR of *S. virgaurea* and *S. gigantea* were greater than those of *S. canadensis*, and the negative effects of increasing sown species richness on RLPR were stronger in *S. canadensis* and *S. virgaurea* than in *S. gigantea* (Fig. 1b, Table 2).

Table 1. Results of linear-mixed effects models for growth-related variables measured in the second study year and relative leaf production rates measured in both study years.

Source of variation	Survival		Flowering		No_{Shoot}		L_{Shoot}		No_{Leaf}	
	χ^2	*P*	χ^2	*P*	χ^2	*P*	χ^2	*P*	χ^2	*P*
Species richness (SR)	**16.65**	**<0.001**	**40.151**	**<0.001**	**69.04**	**<0.001**	**69.08**	**<0.001**	**76.24**	**<0.001**
Functional group number (FG)	**4.45**	**0.035**	1.279	0.258	0.05	0.817	<0.01	0.947	0.21	0.646
Species-ID	**17.49**	**<0.001**	**17.351**	**<0.001**	**56.25**	**<0.001**	**98.47**	**<0.001**	**37.89**	**<0.001**
Species-ID × SR	**16.61**	**<0.001**	1.844	0.398	5.48	0.064	**8.18**	**0.017**	**8.73**	**0.013**
Species-ID × FG	0.67	0.072	0.450	0.7984	0.13	0.936	0.91	0.63454	0.42	0.810
Source of variation	**$Diameter_{Stem}$**		**BM_{Plant}**		**L_{Leaf}**		**SLA**		**LeafG**	
	χ^2	*P*	χ^2	*P*	χ^2	*P*	χ^2	*P*	χ^2	*P*
Species richness (SR)	**80.57**	**<0.001**	**86.03**	**<0.001**	**58.78**	**<0.001**	**79.16**	**<0.001**	**41.04**	**<0.001**
Functional group number (FG)	0.13	0.722	0.39	0.532	0.45	0.501	1.12	0.291	0.02	0.892
Species-ID	1.37	0.504	**34.77**	**<0.001**	**44.41**	**<0.001**	**21.69**	**<0.001**	**237.42**	**<0.001**
Species-ID × SR	**15.98**	**<0.001**	**8.00**	**0.018**	**7.65**	**0.022**	0.47	0.790	**19.08**	**<0.001**
Species-ID × FG	0.50	0.779	2.33	0.311	2.03	0.362	2.69	0.260	1.17	0.556
Source of variation	**$RLPR_{Total}$**		**$RLPR_{Year1}$**		**$RLPR_{Year2}$**					
	χ^2	*P*	χ^2	*P*	χ^2	*P*				
Species richness (SR)	**73.48**	**<0.001**	**54.74**	**<0.001**	**66.22**	**<0.001**				
Functional group number (FG)	0.14	0.707	1.53	0.216	0.02	0.896				
Species-ID	**19.79**	**<0.001**	**263.12**	**<0.001**	**30.47**	**<0.001**				
Species-ID × SR	**6.57**	**0.037**	4.78	0.092	**7.21**	**0.027**				
Species-ID × FG	0.41	0.815	1.15	0.563	1.19	0.552				

Abbreviation of variable names: No_{Shoot} = total shoot number, L_{Shoot} = maximum shoot length, No_{Leaf} = total leaf number, $Diameter_{Stem}$ = basal stem diameter, BM_{Plant} = plant biomass, L_{Leaf} = maximum leaf length, SLA = specific leaf area, LeafG = leaf greenness, $RLPR_{Total}$, $RLPR_{Year1}$, and $RLPR_{Year2}$ = leaf production rate over the whole study period, in the first and in the second study year, respectively. Models were fitted by stepwise inclusion of fixed effects. Shown are the results of likelihood ratio tests (χ^2) that were applied to assess model improvement and the statistical significance of the fixed effects (*P* values). Significant effects are marked with bold letters.

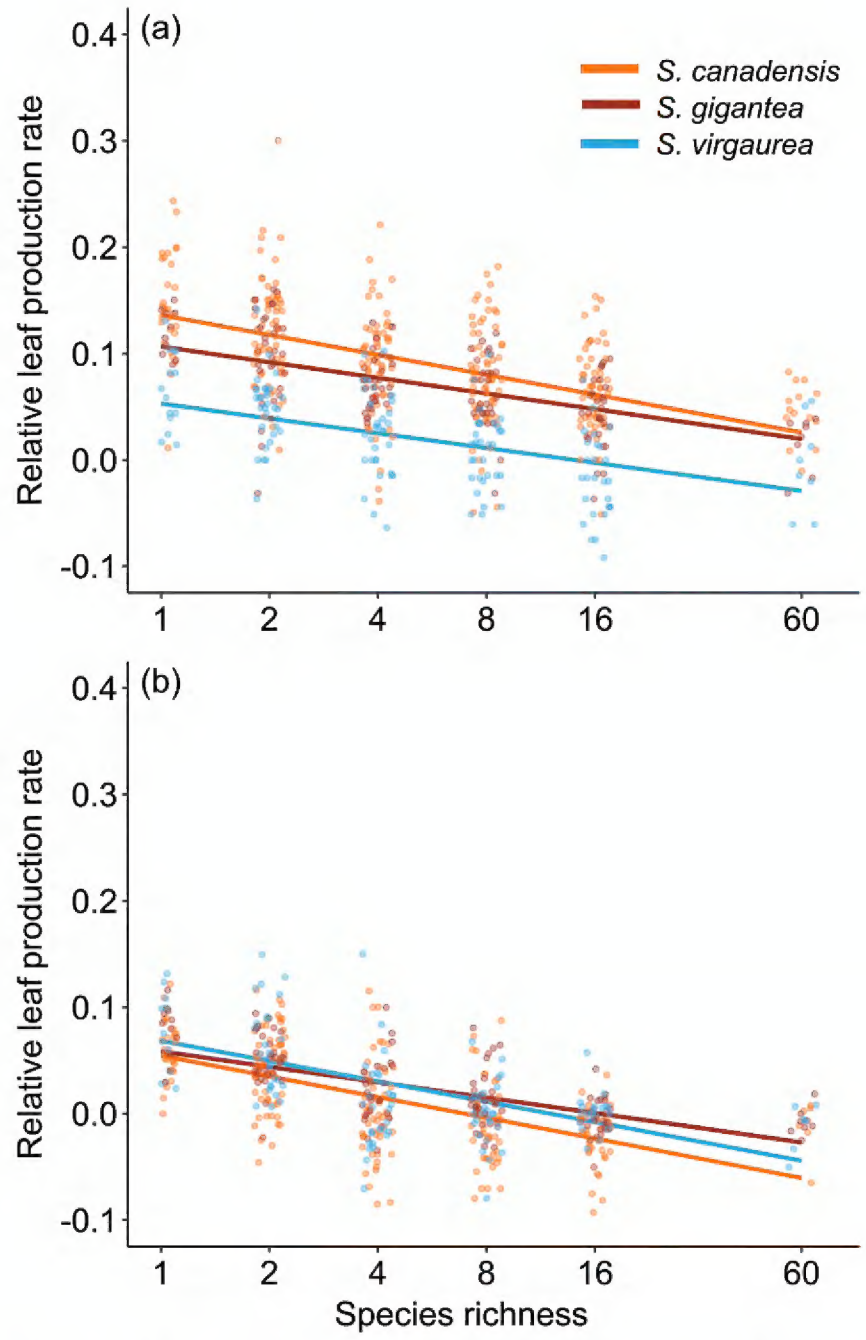

Figure 1. Effects of sown plant species richness of the biodiversity experiment on relative leaf production rate (RLPR) in (**a**) the first study year and (**b**) the second study year. Relationships were analyzed in linear mixed-effects models (Table 1), and regression lines indicate the slope of the plant species richness-effects for each *Solidago* species.

In spite of the smaller RLPR in the second year, total leaf number and length of the longest shoot were greater in the locally common invasive *S. canadensis* than in the locally rare invasive *S. gigantea* and smallest in the native *S. virgaurea* in both years with the exception that the total number of leaves did not differ between both non-native *Solidago* species in the second year (Fig. 2a, b, Table 2 and Suppl. material 1: table S3). Total leaf number and maximum shoot length decreased with increasing sown species richness with the strongest decline in *S. canadensis*, while negative species-richness effects on these size-related variables were weakest in *S. gigantea* and intermediate in *S. virgaurea*. In the first year, most plants did not form more than one or two shoots (only 28 out of 638 cases with more than two shoots). In the second year, the number of shoots was greater in both non-native *Solidago* species than in the native *S. virgaurea* (Table 2). Basal stem diameter of the largest shoot was similar in all three species (Table 2). Both shoot number and stem basal diameter decreased with increasing sown species richness with the strongest response in *S. canadensis* (Suppl. material 1: fig. S3, Table 1). At the final harvest in August 2012, individual plant biomass was similar in *S. canadensis* and *S. gigantea* and in both non-native species greater than in the native *S. virgaurea* (Table 2). Increasing sown species richness had negative effects on individual plant biomass in all *Solidago* species, but again the negative species-richness effects were strongest in *S. canadensis*, but did not differ between *S. virgaurea* and *S. gigantea* (Fig. 2c, Table 1).

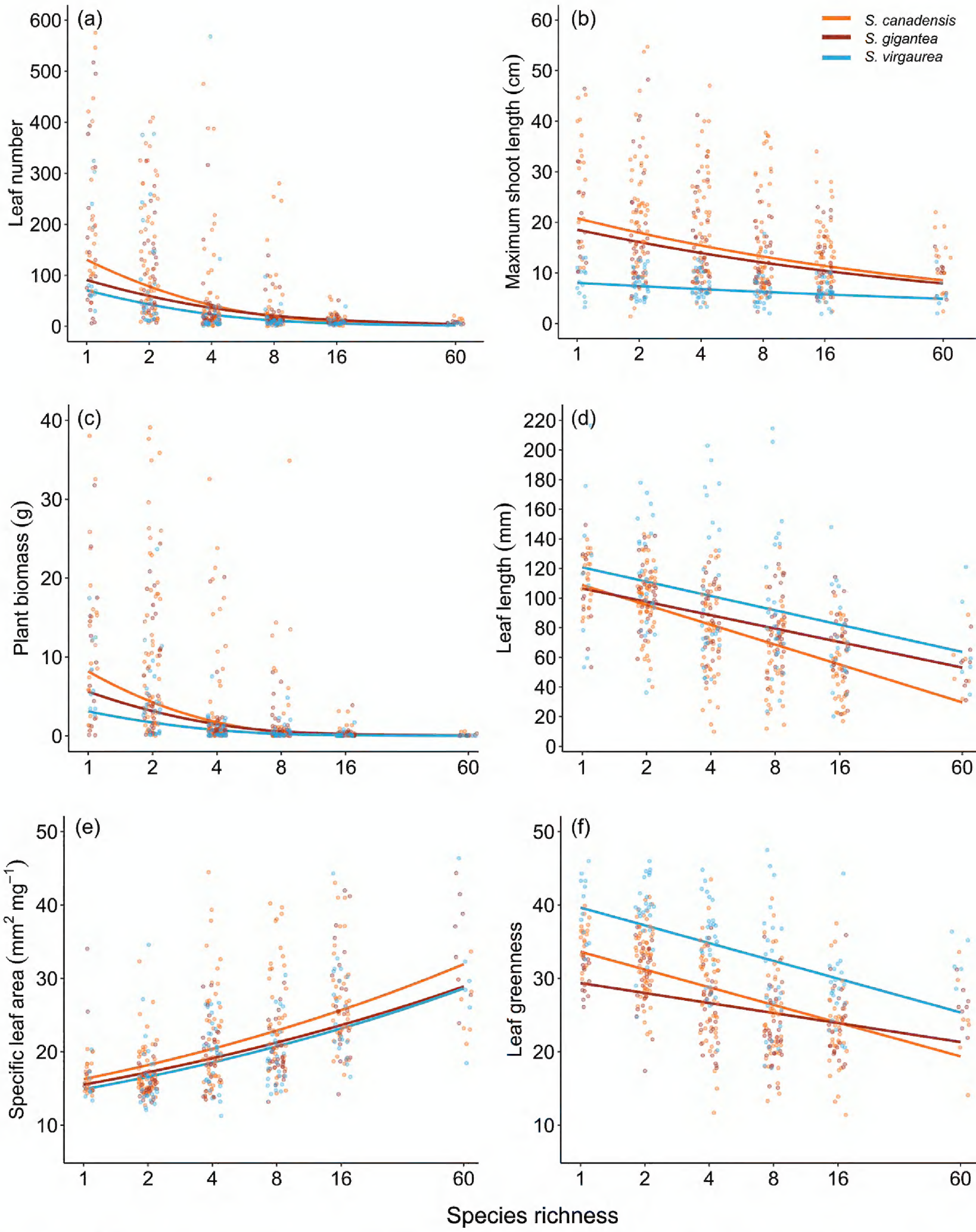

Figure 2. Effects of sown plant species richness of the biodiversity experiment on (**a**) total leaf number, (**b**) length of the longest shoot, (**c**) individual plant biomass, (**d**) maximum leaf length, (**e**) specific leaf area, and (**f**) leaf greenness based on measurements in the second study year. Relationships were analyzed in linear mixed-effects models (Table 1), and regression lines indicate the slope of the plant species richness-effects for each *Solidago* species.

In the first year, both non-native *Solidago* species reached a greater maximum leaf length than the native *S. virgaurea*, while the opposite was the case in the second year, when *S. virgaurea* produced particularly long rosette leaves. In both years and all *Solidago* species, maximum leaf length decreased with increasing sown species richness (Fig. 2d, Table 2 and Suppl. material 1: table S3). In the first year, values for specific leaf area (SLA) were greatest in *S. virgaurea* and decreased in the order *S. virgaurea* > *S. canadensis* > *S. gigantea*. In the second year, values for SLA were

Table 2. Mean values across species-richness levels based on model predictions and standardized regression slopes over species richness for measured continuous variables.

Variable	Year	Mean values			Standardized slopes		
		S. canadensis	*S. gigantea*	*S. virgaurea*	*S. canadensis*	*S. gigantea*	*S. virgaurea*
No_{Shoot}	2nd	**3.6 (±0.2)**	**4.1 (±0.3)**	2.0 (±0.2)	**-0.568 (±0.071)**	-0.531 (±0.073)	-0.397 (±0.084)
L_{Shoot} (cm)	1st	**15.9 (±0.3)**	14.4 (±0.4)	7.1 (±0.2)	**-0.333 (±0.071)**	-0.318 (±0.078)	-0.184 (±0.078)
	2nd	**30.4 (±1.0)**	24.1 (±1.1)	15.8 (±0.8)	**-0.592 (±0.072)**	-0.421 (±0.076)	-0.523 (±0.080)
No_{Leaf}	1st	**23.6 (±0.5)**	15.9 (±0.4)	9.4 (±0.3)	-0.390 (±0.058)	-0.277 (±0.065)	-0.302 (±0.065)
	2nd	**79.2 (±5.4)**	**65.4 (±6.5)**	38.4 (±4.0)	**-0.636 (±0.073)**	-0.482 (±0.076)	-0.609 (±0.079)
L_{Leaf} (mm)	1st	95 (±1)	**110 (±2)**	86 (±2)	-0.476 (±0.080)	-0.491 (±0.086)	-0.429 (±0.086)
	2nd	84 (±1)	87 (±2)	**100 (±2)**	**-0.547 (±0.073)**	-0.369 (±0.079)	-0.395 (±0.084)
$Diameter_{Stem}$ (mm)	2nd	2.80 (±0.07)	2.74 (±0.10)	3.68 (±0.13)	**-0.704 (±0.071)**	-0.473 (±0.075)	-0.606 (±0.243)
BM_{Plant} (g)	2nd	**4.84 (±0.41)**	**4.25 (±0.53)**	1.91 (±0.25)	**-0.677 (±0.071)**	-0.533 (±0.074)	-0.590 (±0.077)
SLA ($mm^2\ mg^{-1}$)	1st	30.4 (±0.4)	28.0 (±0.5)	**32.2 (±0.6)**	0.442 (±0.072)	0.376 (±0.079)	0.401 (±0.079)
	2nd	**20.4 (±0.3)**	20.0 (±0.4)	19.3 (±0.4)	0.561 (±0.073)	0.517 (±0.078)	0.545 (±0.082)
LeafG	1st	26.2 (±0.2)	26.2 (±0.3)	**31.5 (±0.3)**	-0.310 (±0.082)	-0.199 (±0.088)	**-0.418 (±0.088)**
	2nd	29.1 (±0.3)	26.4 (±0.4)	**34.4 (±0.4)**	**-0.497 (±0.080)**	-0.281 (±0.083)	**-0.499 (±0.086)**
$RLPR_{Year1}$	1st	**0.095 (±0.002)**	0.075 (±0.003)	0.023 (±0.003)	-0.491 (±0.065)	-0.330 (±0.073)	-0.311 (±0.073)
$RLPR_{Year2}$	2nd	0.018 (±0.002)	**0.027 (±0.003)**	**0.027 (±0.003)**	**-0.616 (±0.074)**	-0.459 (±0.079)	**-0.604 (±0.082)**
$RLPR_{Total}$	total	**0.041 (±0.002)**	**0.039 (±0.003)**	0.026 (±0.003)	**-0.632 (±0.074)**	-0.495 (±0.078)	-0.606 (±0.081)

Bold letters indicate significantly higher mean values or steeper slopes based on comparisons among species. Abbreviation of variable names: BM_{Plant} = plant biomass, $Diameter_{Stem}$ = basal stem diameter, L_{Leaf} = maximum leaf length, L_{Shoot} = maximum shoot length, No_{Leaf} = total leaf number, No_{Shoot} = shoot number, SLA = specific leaf area, LeafG = leaf greenness, $RLPR_{Total}$, $RLPR_{Year1}$, and $RLPR_{Year2}$ = leaf production rate over the whole study period, in the first and in the second study year, respectively.

greatest in *S. canadensis* and decreased in the order *S. canadensis* > *S. gigantea* > *S. virgaurea* (Fig. 2e, Table 2). SLA increased to a similar extent in all *Solidago* with increasing sown species richness and number of functional groups in both years (Suppl. material 1: table S3). Leaf greenness was greatest in the native *S. virgaurea* and had similar values in the non-native *S. canadensis* and *S. gigantea* in both years (Table 2). In the first year, leaf greenness decreased with increasing species richness with a stronger response in *S. virgaurea* compared to both non-native *Solidago* species. In the second year, the decline in leaf greenness with increasing species richness showed similar strengths in *S. virgaurea* and *S. canadensis* and was less pronounced in *S. gigantea* (Fig. 2f). Plant biomass at final harvest and SLA was negatively correlated (Fig. 3). In both years, community leaf area index and canopy height of resident species rose with increasing species richness (Suppl. material 1: fig. S4).

Discussion

Inherent differences in growth performance among *Solidago* species

While traits promoting a high reproductive output and rapid spread are important for the colonization of new environments, traits related to fast growth and resource acquisition are important for establishment and growth in resident vegetation. The latter is particularly relevant for this study because pre-grown plantlets were planted in the established vegetation of the biodiversity experiment. A taller growth stature, higher growth rates or good survival have been repeatedly reported as characteristics for the success of invasive non-native compared to native plant

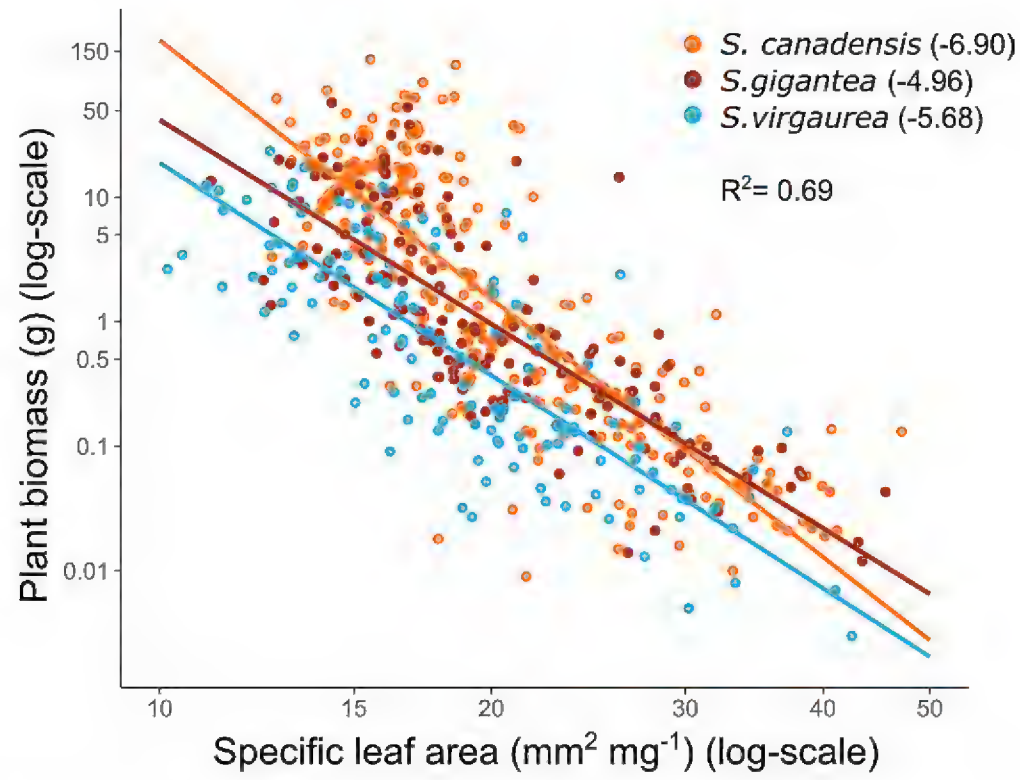

Figure 3. Relationship between plant biomass (log-scale) and specific leaf area (log-scale) based on a linear regression model and measurements taken in the second study year. Numbers in brackets indicate the slope of the biomass-SLA relationship for each species. It was significantly steeper in *S. canadensis* than in *S. gigantea* ($P < 0.001$) and *S. virgaurea* ($P = 0.030$), while it did not differ between the latter two species ($P = 0.350$).

species (van Kleunen et al. 2010). While both non-native *Solidago* species reached a taller growth than *S. virgaurea*, the results for survival and RLPR were mixed. The non-native locally common invasive *S. canadensis* had the highest RLPR in the first year of the experiment, which is in line with findings that non-native species are often characterized by a fast early growth (Dawson et al. 2011). Its RLPR was smaller in the second year, which is not surprising as relative growth rates typically decrease with plant size (Rose et al. 2009). The non-native locally rare invasive *S. gigantea* started with slightly slower RLPR in the first year, but reached higher RLPR in the second year. An inherently slower aboveground growth of *S. gigantea* compared to *S. canadensis* has previously been reported and ascribed to their different belowground architecture and investment in clonal growth. In an experimental study, Schmid et al. (1988) found that *S. canadensis* allocates little biomass to rhizome growth, while *S. gigantea* invests larger amounts of resources into the production of longer rhizomes. Possibly, the greater investment into rhizome growth and higher amounts of belowground reserves could also explain the greater survival of *S. gigantea* compared to *S. canadensis* in the second year in our mown experimental grasslands. The native *S. virgaurea* started with the lowest RLPR in the first year, while its RLPR was higher and not significantly different from that of the non-native *S. gigantea* in the second year. Finally, both non-native *Solidago* species reached on average a higher individual plant biomass than the native *S. virgaurea* at the final harvest in the second year. These results confirm findings from a previous pot experiment showing that single individuals of the non-native invasive *S. canadensis* and *S. gigantea* produce more biomass than those of the native *S. virgaurea* (Szymura and Szymura 2015) and other studies showing that non-native invasive species are often more competitive than native species (Vilà and Weiner 2004; Zhang and van Kleunen 2019). Regarding the measured leaf traits, the native *S. virgaurea* had higher leaf greenness, which is in line with previous studies showing that leaf chlorophyll concentrations are lower in non-native than in native forb species (Scharfy et al. 2011), suggesting a higher light-use

efficiency of non-native invasive forbs. Differences in SLA among the studied *Solidago* species, however, were small and not consistent between study years or related to differences in RLPR. Previous studies also reported that differences in biomass production in congeneric pairs of invasive and non-invasive species are not related to inherent differences in SLA and are probably caused by other traits (Schlaepfer et al. 2010). In summary, the studied *Solidago* species showed inherent differences in growth performance following the expectation that the growth performance of both non-native invasive *Solidago* species is higher compared to the native *S. virgaurea*. Regarding differences between the non-native *Solidago* species, the locally common invasive *S. canadensis* is seemingly faster in early growth, while the locally rare invasive *S. gigantea* reaches a similarly high performance over time.

Plant diversity effects on growth performance of *Solidago* species

Using non-native and native species as invaders in experimentally assembled communities, Sun et al. (2015) found that native species richness only reduced biomass and survival of non-native species, but not of native species. In the present study, increasing species richness did not only decrease individual plant biomass in all three *Solidago* species, but affected all measured growth-related variables, while a higher number of functional groups had only additional negative effects on survival of the *Solidago* individuals. For individual plant biomass, the effects of increased species richness varied between the non-native invasive *Solidago* species and were more pronounced in *S. canadensis* than in *S. gigantea*, while not different in the native *S. virgaurea*. This was mainly due to the particularly high performance of *S. canadensis* at low plant species richness while performance differences among the *Solidago* species were minor in communities with high species richness. Remarkably, the growth performance of the invaders in terms of individual plant biomass and other measured variables was not always higher in plant communities of low species richness, but showed a large variation. These findings imply that grassland species assembled in the biodiversity experiment vary greatly in their capability to suppress the growth of invaders, and that both a higher number of species and the greater probability to include species with high invasion resistance play a role for diversity-invasion resistance relationships.

Having traits conferring a fast-growth life history is especially advantageous in high-resource environments (Reich 2014). Thus, the potential for higher RGR could explain that especially *S. canadensis* capitalized on the greater share of unused resources in plant communities of low species richness, while this was only possible to a lesser extent for the aboveground growth of *S. gigantea*. In line with the general observations in the Jena Experiment (Weisser et al. 2017), canopy density and height measured in the study plots increased with increasing species richness in both years. The taller and denser canopy suggests that light competition is increased at higher plant species richness. Light competition is generally thought to be of crucial importance for the invasion success of non-native plant species in established vegetation (Gioria and Osborne 2014). Du et al. (2017) showed that shaded *S. canadensis* plants had a taller growth, a lower basal stem diameter, and longer and wider leaves with higher chlorophyll contents, rates of photosynthesis and stomatal conductance than without shade. Several studies in grassland biodiversity experiments have shown that most resident plant species increase their growth height and form leaves with a greater SLA in plant communities of higher species richness (e.g. Lipowsky et al. 2015; Roscher et al. 2018). In the present experiment, all

Solidago species produced shorter shoots and leaves in more diverse plant communities, while one would have expected the opposite as a shade-avoidance response (Bell and Galloway 2007). The increased values of SLA with increasing species richness, however, could indicate a shade-tolerance response (Valladares and Niinemets 2008) and might help to enhance the efficiency of light capture in the taller and denser vegetation. The effects of community species richness on shoot morphological traits and leaf greenness were strongest in *S. canadensis*, which is concordant with the more pronounced negative effects of sown species richness on the performance of this species, which was not only reflected in a decline of individual plant biomass but even in a lower survival at higher species richness. On the contrary, plasticity in SLA in response to increased species richness did not differ among *Solidago* species in both study years. The negative relationships between SLA and individual plant biomass, however, indicated that the plasticity in SLA in response to increased species richness is not adaptive, but more likely reflects a passive response (Liu et al. 2016). Another possible cause for the negative effects of species richness on the establishment and growth of the *Solidago* individuals at higher plant species richness are changes in biotic interactions. For example, invertebrate herbivory measured as damaged leaf area and consumed biomass has been shown to increase with sown species richness (e.g. Meyer et al. 2017). This could also have contributed to the reduced survival and growth of the *Solidago* individuals in plant communities of higher sown species richness, but was not quantified in the current study.

In summary, all three *Solidago* species decreased their performance with increasing species richness of the grassland communities, confirming the biotic resistance hypothesis. However, in line with the initial expectations, both non-native invasive *Solidago* species experienced a more pronounced reduction in their growth performance than the native *S. virgaurea* with increasing species richness, indicating that their competitive superiority strongly decreases in plant communities with high resident species richness.

Conclusions

The two-year study showed that inherent differences in growth-related traits led on average to a higher performance of the invasive non-native *Solidago* species in low-diversity communities. At high plant species richness, the performance of all *Solidago* species was similarly low, suggesting that a greater biotic resistance of more diverse plant communities can eliminate the inherent superiority of non-native invasive species. The study presented here is limited to the case of one native vs. two non-native *Solidago* species and the invaders were introduced by planting in the established plant communities at a single experimental site with specific environmental conditions. Despite these limitations, the results emphasize the important role of native plant diversity for invasion resistance at local scale.

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Additional information

Conflict of interest

The author has declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Use of AI

No use of AI was reported.

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Author contributions

The author solely contributed to this work.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Additional figures and tables supporting the results

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Explanation note: **fig. S1.** Illustration of the experimental design. **fig. S2.** Effects of sown plant species richness of the biodiversity experiment on the proportion of surviving phytometers in the second study year. **fig. S3.** Effects of sown plant species richness of the biodiversity experiment on shoot number and basal shoot diameter in the second study year. **fig. S4.** Effects of sown plant species richness of the biodiversity experiment on canopy height and leaf area index of the resident communities. **table S1.** Plant species pool of the Jena Experiment including assignment of species to functional groups (Roscher et al. 2004). **table S2.** Number of experimental plant communities at each level of sown plant species richness and functional group number. **table S3.** Results of linear-mixed effects models for growth-related variables measured in both study years.

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